

ecology are examined in order to evaluate which theories of lycopoid evolution most closely explain the currently recognized pattern.

PALEOZOIC ISOETALEANS

Although most arborescent lycopoids are associated with *Stigmara*, a number of them lack an extensive branched rooting system. The Devonian lycopoid *Lepidosigillaria* is interpreted as a sparsely branched tree over 5 m tall that has a rounded plant base bearing characteristic stigmarian rootlets (Fig. 9A, Table 1; White, 1907; Kräusel & Weyland, 1949). Another Devonian form, *Cylostigma kiltorkense* Haughton, has been reported to have a bilobed plant base (Fig. 9C, Table 1; Johnson, 1913; Schweitzer, 1969; Chaloner, 1984). Unfortunately, the basal part of the stem is abraded, and evidence for this interpretation is difficult to assess (Pigg & Taylor, 1985). An unnamed lycopoid in the Upper Devonian Cleveland Shale also has a lobed or rounded plant base (Fig. 9D, Table 1; pl. I of Chitaley, 1982, 1988). This slender plant is very similar to Mesozoic *Pleuromeia* stems and may represent some of the earliest evidence for the unbranched habit so common in isoetaleans (Chitaley, 1982, 1988). Also found in Devonian strata are stumps described as the bases of the progymnosperm *Eospermatopteris erianus* (Dawson) Goldring (Fig. 9B, Table 1; Goldring, 1924). These plant bases are remarkably similar to those of *Lepidosigillaria* (Fig. 9A, B, Table 1; Goldring, 1924; fig. 8.17 of Gensel & Andrews, 1984). Because these stumps have not been found attached to other parts of the plant, the possibility that some specimens belong to isoetalean, rather than progymnospermous, plants should not be overlooked.

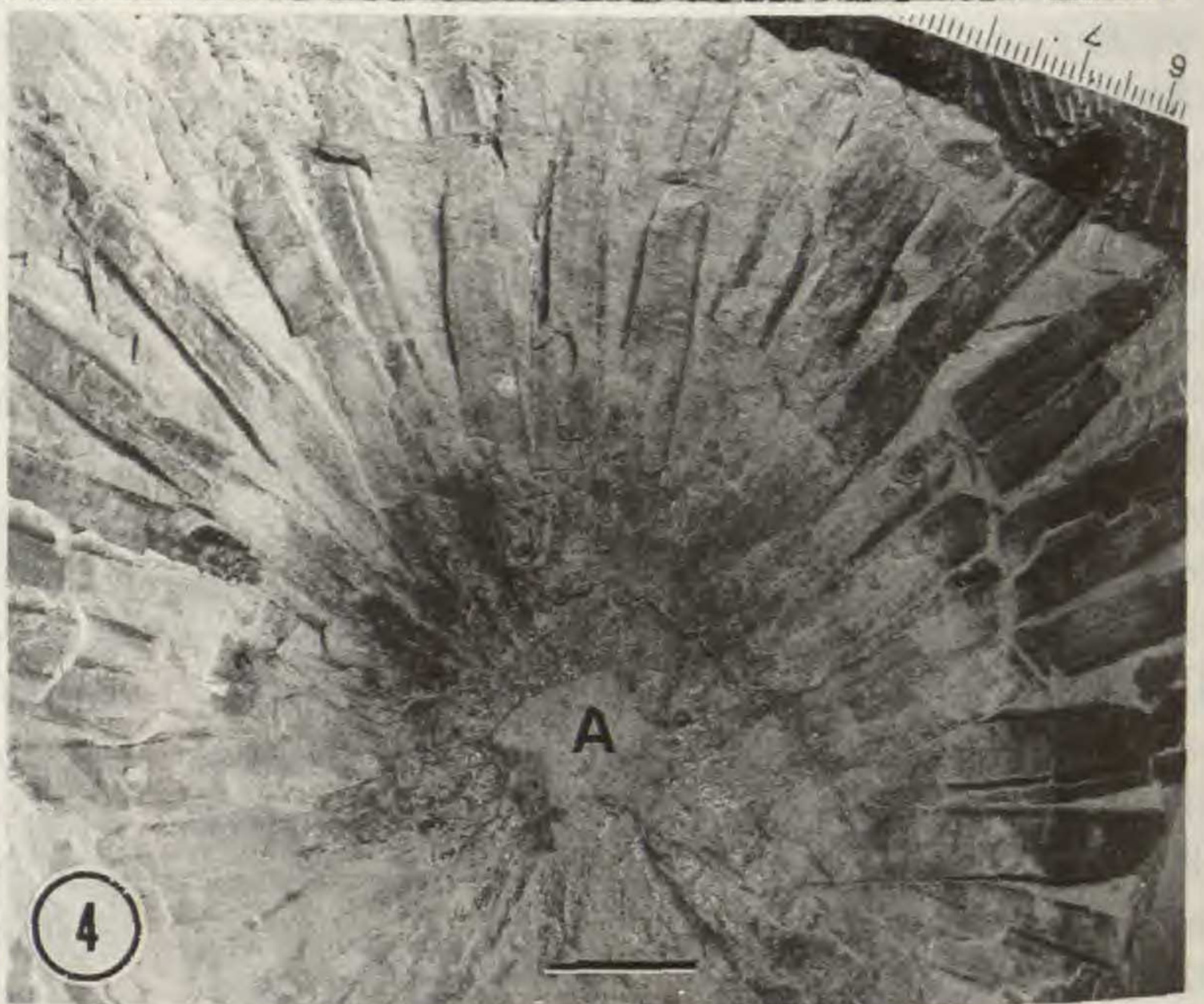
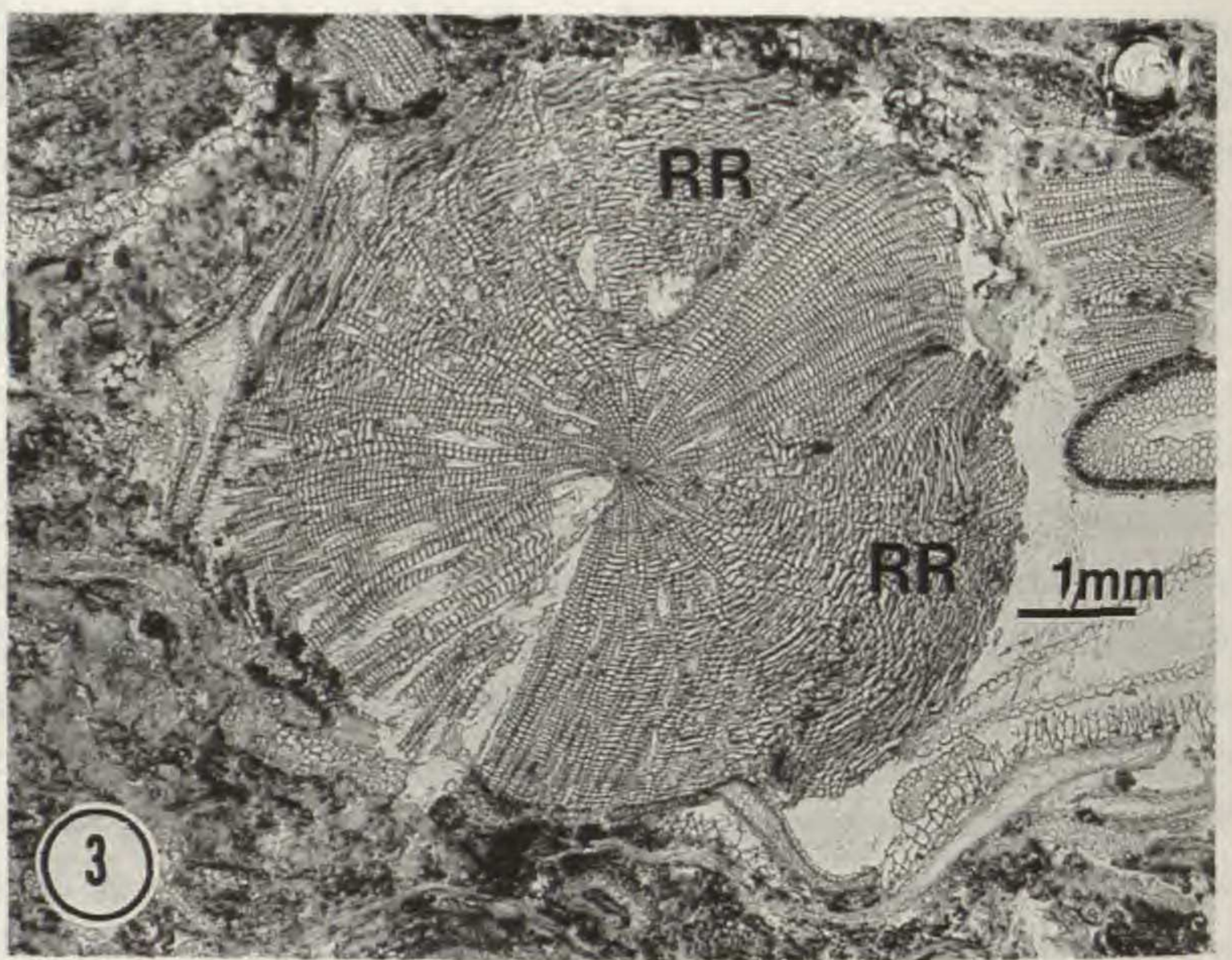
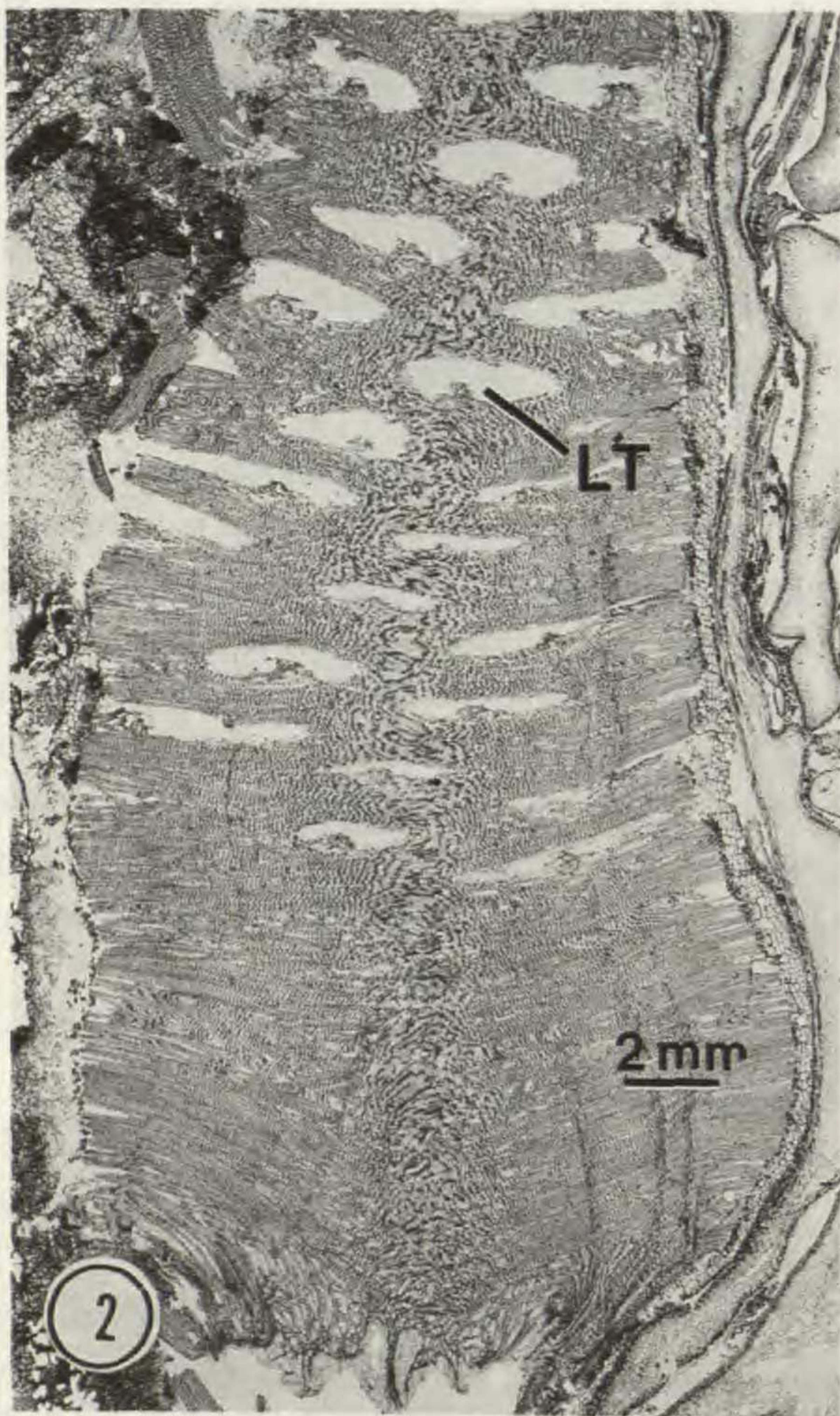
Protostigmara eggertiana Jennings, a plant base with up to 13 lobes, is known from Lower Mississippian strata in Virginia (Fig. 9E, Table 1; Jennings, 1975; Jennings et al., 1983). *Protostigmara* is characterized by a basal pattern of lobes and furrows comparable to the pattern in the base of a multilobed *Isoetes*. In this pattern, cortical lobes occur between the juncture of three furrows. Apart from isoetalean and stigmarian-bearing lycopoids, this regular pattern of lobes and furrows is unknown in rooting systems of vascular plants. *Protostigmara* presumably grew in a manner similar to that of a multilobed *Isoetes*, by adding new lobes between bifurcations of the furrows (Jennings et al., 1983). *Protostigmara* has been found in attachment to the lepidodendrid stem *Lepidoden-*

dropsis Lutz (Jennings et al., 1983). This tall, much-branched tree would have required an anchoring mechanism of some type. The plant may have accomplished this by effectively "burying" its rooting system, as does *Isoetes* (Karrfalt, 1977), with the production of new roots from the furrows and the resulting lateral displacement of older roots (Jennings et al., 1983).

While descriptions of *Lepidosigillaria*, *Protostigmara*, and other forms demonstrate diversity in rooting structure among tree lycopoids (Fig. 9E), these plants are not known in anatomical detail. The relationship of these earlier lycopoids to later isoetalean/lepidodendrid lineages cannot yet be clarified. The discovery of internal anatomy and reproductive organs would greatly enhance our understanding of these plants and their role in rhizomorphic lycopoid radiation.

The presence of isoetalean lycopoids in the Carboniferous was clearly established with the description of the anatomically preserved lycopoid *Chaloneria cormosa* Pigg & Rothwell and the recognition of the Chaloneriaceae (Figs. 2, 3, 9F, Table 1; Pigg & Rothwell, 1979, 1983a, b; DiMichele et al., 1979). *Chaloneria cormosa* was described from the Upper Pennsylvanian coal ball flora of North America as a plant with internal tissues that are similar to those of the lepidodendrids but lacking a stigmarian rooting system (Figs. 2, 3, 9F; Pigg & Rothwell, 1979, 1983a). Instead, *C. cormosa* has a bilaterally symmetrical, cormlike plant base that resembles that of modern *Isoetes*.

Stems of *C. cormosa* are up to 10 cm in diameter and have an exarch protostele that begins at the base of the plant as a tiny rod of tracheids (Fig. 3) and expands distally, becoming medullated at higher levels (Pigg & Rothwell, 1979). No branching specimens are known. Primary xylem is somewhat fluted like that of *Sigillaria approximata* Fountaine & White (Delevoryas, 1957) and consists of metaxylem with tracheids with scalariform and reticulate wall thickening patterns separated by plates of xylem parenchyma, and protoxylem with helical wall thickening patterns (Pigg & Rothwell, 1983a). *Chaloneria cormosa* produces a thick zone of secondary xylem at the base (Figs. 2, 3) that is absent at distal-most levels. Since plant bases are decorticated, the entire size of the plant base and details of its external morphology are unknown. Wood of *Chaloneria* has uniseriate rays and tracheids with reticulate wall thickening patterns. Secondary tracheids in the basal region of the stem may be branched and contorted. To the outside of the xylem is a cylinder of phloem composed of



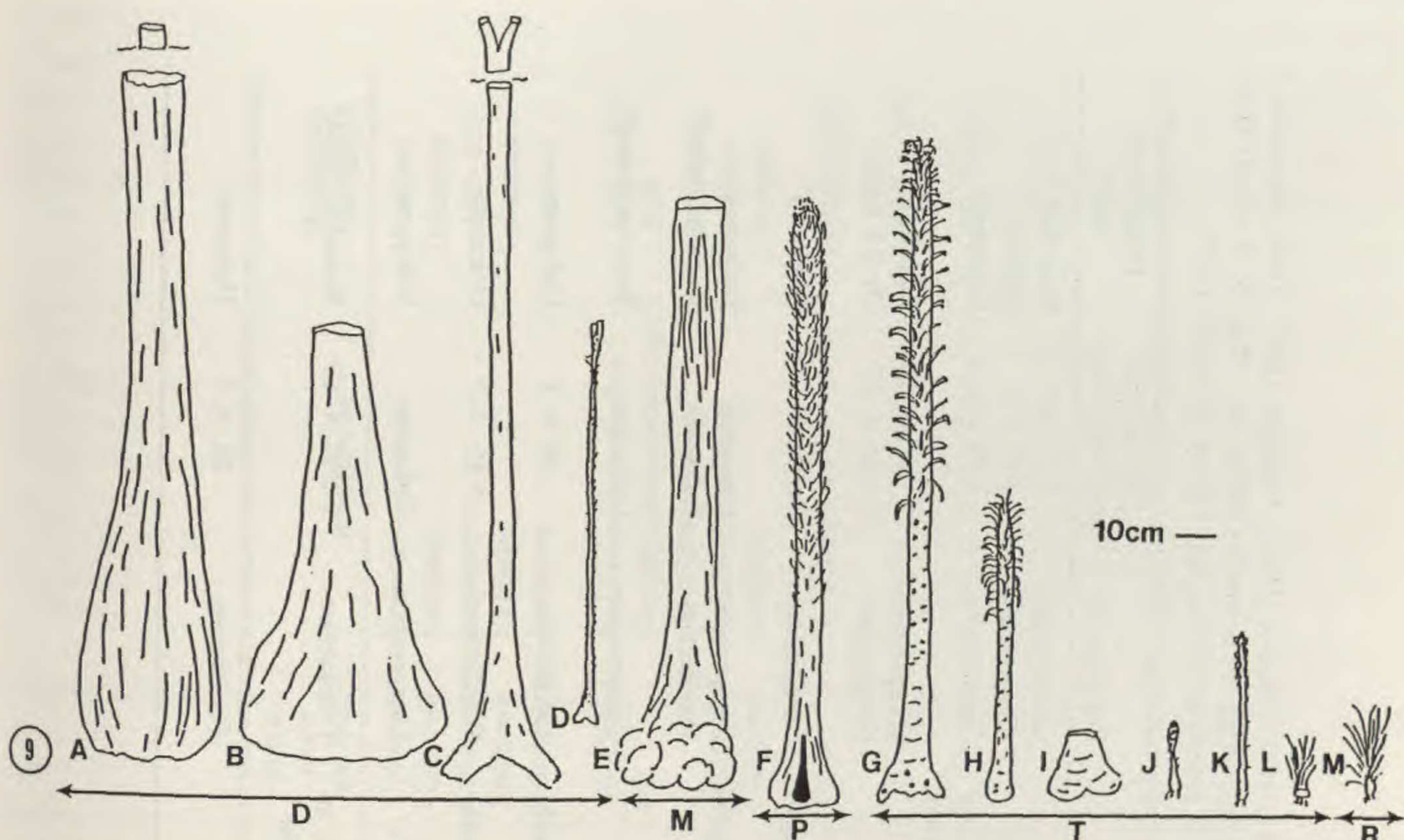


FIGURE 9. Reconstructions of isoetalean lycopoids from the Paleozoic, Mesozoic, and Cenozoic, drawn to scale (bar = 10 cm). A = *Lepidosigillaria whitei* (redrawn from White, 1907); B = *Eospermatopteris textilis* (redrawn from Gensel & Andrews, 1984); C = *Cyclostigma kiltorkense* (redrawn from Johnson, 1913); D = unnamed Cleveland Shale lycopoid (redrawn from Chitaley, 1982); E = *Protostigmaraia eggertiana* (redrawn from Jennings et al., 1983); F = *Chaloneria cormosa* (redrawn from Pigg & Rothwell, 1983a); G = *Pleuromeia sternbergi* (redrawn from Mägdefrau, 1931); H = *Pleuromeia rossica* (redrawn from Neuburg, 1960); I = *Takhtajanodoxa* (redrawn from Snigirevskaya, 1980a); J, K = *Pleuromeia jiaochengensis* (redrawn from Wang & Wang, 1982); L = *Isoetes gramineoides* (redrawn from Bock, 1962); M = *Isoetes* sp., extant. Reconstructions are organized stratigraphically: D = Devonian, M = Mississippian, P = Pennsylvanian, T = Triassic, R = Recent. Dimensions were obtained from the literature. It should be pointed out that previously *Eospermatopteris* (B) has not been considered a lycopoid. The reconstruction of *Cyclostigma kiltorkense* (C) is highly conjectural because of the poor preservation of the material. The reconstruction of *Chaloneria cormosa* (F) is based on size estimated from external cortical tissues with the anatomically preserved woody base indicated by the shaded area.

sieve cells and parenchyma. Cortical tissues include a combination of primary, parenchymatous zones, secondary periderm from a distinct lateral cortical cambium, and irregular proliferations of secondary growth resulting from internal cell divisions of pri-

mary cortical cells. The last two cortical types, when seen together in tangential section, result in patterns referable to the decortication forms *Knorria* Sternberg and *Asolanus* Wood, respectively (Pigg & Rothwell, 1983a, 1985).

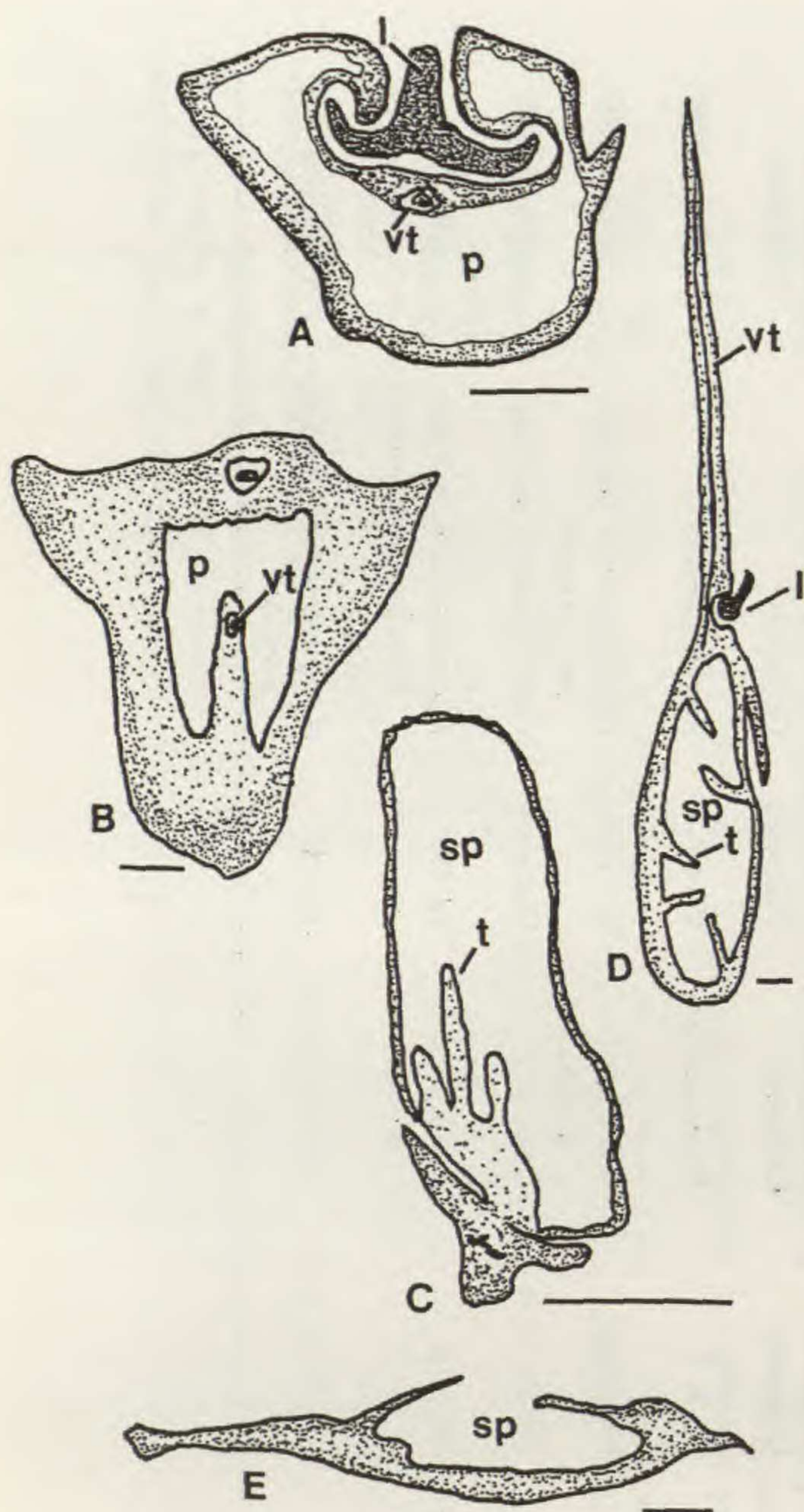
FIGURES 2-8. Representative isoetalean lycopoids of Paleozoic, Mesozoic, and Cenozoic ages. 2, 3. *Chaloneria cormosa*. —2. Longitudinal section through decorticated plant base showing abundant secondary xylem, helically arranged leaf traces (LT), and root traces. 1423 E Bot. #23, PHOU, $\times 3.3$. —3. Cross section through the base of the stem. Primary body is reduced to a tiny central point, areas of the rooting region (RR) extend upward on either side. 1387 Q(2) Top #2, PHOU, $\times 8$. —4. Vertically compressed specimen of *Cylomeia* from the Triassic of Australia, showing a crown of vegetative leaves radiating from the axis (A). AMF 58791, AM, $\times 1$. —5. *Isoetites serratus*, Cenozoic isoetalean from the Cretaceous of Wyoming. Crown of leaves that have been compressed vertically around plant axis (A). Type specimen. USNM 315170, $\times 1$. —6. Plant base of *Cylomeia*-type Triassic lycopoid. AMF 59985, AM, $\times 1$. —7. *Isoetites serratus* leaf. Higher magnification of Figure 5 to show detail of impressions of air channels (T) and serrate margin of sporophylls. Type specimen. USNM 315170, $\times 4$. —8. Extant *Isoetes* sp. plant base with attached roots, $\times 2$. Scale bars = 1 cm unless otherwise indicated. (PHOU = Paleobotanical Herbarium, Department of Botany, Ohio University, Athens, Ohio; USNM = U.S. National Museum, Smithsonian Institution, Washington, D.C.; AM = The Australian Museum, Sydney, New South Wales, Australia.)

TABLE 1. Paleozoic isoetalean lycopsids. Data taken from the following sources: ¹ Kräusel & Weyland (1949); ² Johnson (1913); ³ Chitaley (1982, 1988, unpublished data); ⁴ Goldring (1924); ⁵ Jennings (1975); Jennings et al. (1983); ⁶ Chaloner (1958); ⁷ Dräbek (1976); ⁸ Pigg & Rothwell (1983a, b); ⁹ Pigg & Taylor (1985); ¹⁰ Leisman (1970); ¹¹ DiMichele et al. (1979), Pigg & Rothwell (1983 a, b); ¹² Abbott (1963); ¹³ Pigg & Rothwell (1983 a, b); ¹⁴ Remy & Remy (1975).

Taxon	Age	Occurrence	Extent	Preservation	Stem length and width (cm)	Rhizomorph shape
<i>Lepidosigillaria whitei</i> ¹	Devonian	New York, U.S.A.	Stem and plant base	Compression	>500 × 7	Rounded
<i>Cyclostigma kiltorkense</i> ²	Devonian	Ireland	Stem and ?plant base	Compression	>800 × 7	Bilobed?
Unnamed lycopsid ³	Devonian	Ohio, U.S.A.	Stem and plant base and attached fructification	Compression	119 × 1.5	Rounded
<i>Eospermatopteris textilis</i> ⁴	Devonian	New York, U.S.A.	Stem and plant base	Compression	? × 25	Rounded?
<i>Protostigmaria eggertiana</i> ⁵	Mississippian	Virginia, U.S.A.	Stem and plant base	Compression	>166 × 17	10–13 lobes
<i>Polysporia mirabilis</i> ⁶	Westphalian A–C	England, Scotland, United States	Fructification with spores	Compression	Unknown	Unknown
<i>Polysporia robusta</i> ⁷	Westphalian C	Central Bohemia	Fructification with spores	Compression	Unknown	Unknown
<i>Chaloneria</i> sp. ⁸	Middle Pennsylvanian	Ohio, U.S.A.	Stem and plant base, spores	Petrifaction	Unknown	Rounded/lobed?
<i>Cormophyton mazonensis</i> ⁹	Middle Pennsylvanian	Illinois, U.S.A.	Stem and plant base	Compression	Unknown	Rounded/lobed?
<i>Sporangiostrobus kansanensis</i> ¹⁰	Middle Pennsylvanian	Kansas, U.S.A.	Stem; fructification with spores	Petrifaction	40 × ?	Unknown
<i>Chaloneria periodica</i> ¹¹	Middle Pennsylvanian	Kentucky, Illinois, Indiana, U.S.A.	Stem; fructification with spores	Petrifaction	>15 × ?	Unknown
<i>Lepidostrobopsis missouriensis</i> ¹²	Middle–Late Pennsylvanian	Oklahoma, U.S.A.	Megasporophylls with spores	Compression	Unknown	Unknown
<i>Chaloneria coromosa</i> ¹³	Late Pennsylvanian	Ohio, U.S.A.	Stem with plant base, attached fructification with spores	Petrifaction	>200 × 10	Rounded/lobed?
<i>Sporangiostrobus puertollanensis</i> ¹⁴	Late Stephanian	Spain	Stem	Petrifaction	21 × ?	Unknown

TABLE 1. Continued.

Taxon	Rhizomorph width (cm)	Fertile zone length × width (cm)	Size sporangium length × width (mm)	Microspores	Microspore size (μm)	Megaspores	Megaspore size (μm)
<i>Lepidosigillaria whitei</i> ¹	38.5	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
<i>Cyclostigma kiltorkense</i> ²	24	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Unnamed lycopsid ³	2.5	8.4 × 2	12 × 3	Unknown	Unknown	Immature?	400-475
<i>Eospermatopteris textilis</i> ⁴	60	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
<i>Protostigmaria eggertiana</i> ⁵	32	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
<i>Polysporia mirabilis</i> ⁶	Unknown	>7 × 7	13-30 × 7	<i>Endosporites</i>	66-175	<i>Valvisporites auritus</i>	520-1,360
<i>Polysporia robusta</i> ⁷	Unknown	>14 × 5.5	6-10 × 4-6	<i>Endosporites</i>	61	<i>Pseudovalvisporites</i> var. <i>sculptus</i>	1,200
<i>Chaloneria</i> sp. ⁸	1.2 (decorticated)	Unknown	Unknown	<i>Endosporites</i>	Unknown	<i>Valvisporites</i>	Unknown
<i>Cormophyton mazonensis</i> ⁹	2.6	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
<i>Sporangiostrobus kansanensis</i> ¹⁰	Unknown	>16 × 12	11 × 7	<i>Densosporites</i>	39-57	<i>Zonalesporites</i>	2,500-3,000
<i>Chaloneria periodica</i> ¹¹	Unknown	>8 × ?	Unknown	<i>Endosporites globiformis</i>	67-140	<i>Valvisporites auritus</i> var. <i>grandis</i>	900-1,560
<i>Lepidostrobopsis missouriensis</i> ¹²	Unknown	Unknown	18-25 × 8-12	Unknown	Unknown	<i>Valvisporites auritus</i>	1,000-1,500
<i>Chaloneria cormosa</i> ¹³	1.9 (decorticated)	>21 × 10	6 × 2	<i>Endosporites globiformis</i>	48-87	<i>Valvisporites auritus</i> ; <i>Pseudovalvisporites auritus</i>	430-670
<i>Sporangiostrobus puertollanensis</i> ¹⁴	Unknown	? × 3	9-10 × 4-5	<i>Densosporites</i>	40-60	<i>Zonalesporites</i> ; <i>Cristatisporites</i>	Unknown



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FIGURE 10. Line diagrams of isoetalean leaf bases and sporophylls. —A. Transverse section through leaf base of *Takhtajanodoxa*. Note ligule (l) with glossopodium, vascular tissue (vt), and large air channel (p). Redrawn from Snigirevskaya (1980a) $\times 13$. —B. Transverse section through leaf base of *Chaloneria cormosa*. Note small ligule (at top), bifurcating parichnos strand (p), and vascular tissue (vt) $\times 7.3$. —C. Transverse section through sporophyll of *Chaloneria cormosa* showing position of trabeculae (t) in the sporangium (sp). B and C redrawn from Pigg & Rothwell (1983a). —D. Longitudinal section through sporophyll of *Isoetes* to show position of ligule (l) with glossopodium, vascular tissue (vt), sunken sporangium (sp) with trabeculae (t), and velum (at right) $\times 4$. —E. Transverse section through sporangium (sp) of *Pleuromeia rossica* to show sunken nature of sporangium. Redrawn from Neuburg (1960) $\times 8$. Scale bars = 1 mm on each figure.

Leaves of *C. cormosa* are ligulate and have a single bilobed, or double vascular trace accompanied by parichnos channels that bifurcate proximally and diminish distally (Fig. 10B). Abaxial, sunken stomata occur in rows. The fertile region of *C. cormosa* is up to 21 cm long and consists of broad zones of alternating micro- and megasporangia (Pigg & Rothwell, 1983a). Sporophylls bear sporangia 6 mm long \times 2 mm wide on the adaxial surface. Microsporangia have abundant trabecular tissue (Fig. 10C) and bear hundreds of microspores, both singly and in tetrads, of the pseudosaccate *Endosporites* Wilson & Coe type (Wilson & Coe, 1940). Megasporangia, also with trabeculae, bear up to several hundred auriculate spores referable to *Valvisporites auritus* (Zerndt) Potonié & Kremp that grade into the nonauriculate form *Pseudovalvisporites* Lachkar (Drábek, 1976).

Cellular megagametophytes have been discovered within *Chaloneria* megaspores (Pigg & Rothwell, 1983b). They are composed of large central and small peripheral parenchymatous cells and contain up to about a dozen archegonia at various developmental stages showing two, three, or four tiers of neck cells. Mature gametophytes protrude out the trilete haplotypic mark and may produce a few rhizoids. Fungal hyphae also occur in the gametophyte tissue (Pigg, pers. obs.). The biological role of these fungi, that is, whether they were saprophytes, parasites, or mycorrhizae, has not been addressed. *Chaloneria* megagametophytes are very similar to those previously described for fossil and extant heterosporous lycopsids (La Motte, 1933; Brack, 1970; Galtier, 1970; Phillips, 1979; Stubblefield & Rothwell, 1981; Pigg & Rothwell, 1983b).

A second species, *C. periodica* Pigg & Rothwell (= *Polysporia mirabilis* Newberry sensu DiMichele et al., 1979) from Middle Pennsylvanian strata of the Illinois Basin, shares anatomical similarities with *C. cormosa* (Pigg & Rothwell, 1983a). This plant differs from the Upper Pennsylvanian form in having alternating vegetative and fertile zones, larger megaspores, and ligule pits lined with palisadelike cells (DiMichele et al., 1979). The smaller amount of secondary xylem found in this plant probably reflects the limited levels of the stem from which material is known. Basal parts of the plant have yet to be discovered (Pigg & Rothwell, 1983a). Similar permineralized *Chaloneria* fossils are also known from the Middle Pennsylvanian Anderson coal of Ohio (Pigg & Rothwell, 1983a) and have been observed in Lewis Creek, Kentucky (Copland coal) coal balls (Pigg, pers. obs.).

Because of the detailed information known for

Chaloneria, it has been possible to further correlate its structures with a number of less known, disarticulated fossils that also represent the Chaloneriaceae (Table 1). These include compressions of reproductive structures (*Polysporia*, *Lepidostrobopsis* Abbott; Chaloner, 1958; Abbott, 1963; Drābek, 1976), isolated sporangia (*Lepidocystis* Lesquereux; Gastaldo, 1981), isolated rhizomorphs (*Cormophyton* Pigg & Taylor; Pigg & Taylor, 1985), several taxa of decorticated stems (*Asolanus*, *Knorria*; Pigg & Rothwell, 1985), and the spores *Endosporites* (Brack & Taylor, 1972) and *Valvisporites* (Gastaldo, 1981; Taylor, 1990). Based on the widespread distribution of these disarticulated organs in a variety of depositional environments (i.e., freshwater clastic swamp, peat-accumulating swamp, ironstone nodules), together with the stratigraphic record of the spores, it is obvious that *Chaloneria*-type, isoetalean plants were widespread components of the Pennsylvanian flora (Table 1).

Compressed fertile structures bearing *Valvisporites* megaspores and *Endosporites* microspores were united under the genus *Polysporia* by Chaloner based on the presence of these characteristic spore types (Chaloner, 1958). *Polysporia mirabilis* is recognized in Westphalian A to Middle Pennsylvanian sediments in Scotland, England, and the Appalachian and Illinois Basins. Most of the specimens of *P. mirabilis* described by Chaloner (1958) were bisporangiate, although monosporangiate fructifications with these spore types cannot be precluded (Table 1). A second species, *P. robusta* Drābek, which is twice as large (14 cm long) and bears larger megaspores that lack well-defined auriculae (*Pseudovalvisporites*), was later recognized from Bohemia (Table 1; Drābek, 1976). It is interesting that in both permineralized and compressed remains of the Chaloneriaceae, authors refer to the specimens as "fertile regions" rather than compact cones (e.g., Chaloner, 1958; Drābek, 1976; Pigg & Rothwell, 1983a). Often the distal lamina are missing and the large (1.3–3 cm long) sporangia give *Polysporia* a distinctive appearance (e.g., plate 31, fig. 7 of Chaloner, 1958). Pennsylvanian strata also contain isolated sporangia with *Valvisporites* megaspores, assignable to the genus *Lepidocystis* (Gastaldo, 1981); detached sporophylls bearing sporangia with *Valvisporites* megaspores, assignable to *Lepidostrobopsis* (Table 1; Abbott, 1963); and isolated sporangia with *Endosporites* microspores (e.g., Brack & Taylor, 1972). The characteristic spore types *Valvisporites* and *Endosporites* have been described ultrastructurally by Gastaldo (1981) and Taylor

(1990), and Brack & Taylor (1972), respectively. In addition to compressed fertile structures, *Cormophyton*, a mold-cast lycopsid plant base, has been described from the Middle Pennsylvanian Mazon Creek nodule flora (Table 1; Pigg & Taylor, 1985). This wide record of distribution indicates that Paleozoic isoetaleans may have occupied a number of depositional sites both within the peat-accumulating coal swamps and in other freshwater, clastic-dominated wetlands.

Anatomically preserved and compressed plant fructifications and vegetative stems described under the genera *Sporangiostrobus* Bode, *Puertollania* Remy & Remy, and *Bodeodendron* Wagner & Spinner have a suite of similar features when compared to the *Chaloneria/Polysporia* group (Table 1; Němejč, 1931; Leisman, 1970; Remy & Remy, 1975; Wagner & Spinner, 1976; Wagner, 1989). These fossils also are interpreted to represent unbranched or sparsely branched plants of about 1–2 m in height that bear fertile regions rather than compact cones (Wagner, 1989). *Sporangiostrobus* bears megaspores with an equatorial cingulum assignable to *Zonalesporites* Ibrahim and microspores of the widespread, cingulate trilete *Densosporites* Berry type (Leisman, 1970; Remy & Remy, 1975). Anatomically preserved stems originally recognized as *Lepidodendron dacrydioides* Leisman have been allied with *Sporangiostrobus kansanensis* Leisman fertile remains and share structural similarities with *Chaloneria* (Leisman, 1970; Leisman & Stidd, 1977). Because of all of these similarities, *Sporangiostrobus* was interpreted as a member of the Chaloneriaceae (Pigg & Rothwell, 1983b). *Sporangiostrobus* is known in considerably less anatomical detail than other members of the family, but the vegetative parts are found abundantly as compressions, allowing for a detailed description of vegetative form (Wagner, 1989).

Another Pennsylvanian fructification that may have some affinity with the Chaloneriaceae is the genus *Porostrobus* Nathorst. This bisporangiate lycopsid cone bears *Setosisporites* Potonié & Kremp megaspores and *Densosporites* microspores (Leary & Mickle, 1989). Although the microspores are similar to those of *Sporangiostrobus*, the megaspores have a prominent gula and equatorial hairs rather than auriculae like *Valvisporites* or a flangelike cingulum like *Zonalesporites*. *Setosisporites* megaspores of *Porostrobus nathorstii* from early Pennsylvanian strata in Illinois resemble ultrastructurally the megaspores of *Setosisporites praetextus* forma *minor* Chaloner that characterize the cone of *Bothrodendrostrobus*

mundus. This latter genus represents a Lower Pennsylvanian lycopsid cone from England containing megagametophytes with vascularized embryos that demonstrate reproductive biology and embryogeny very similar to that of extant *Isoetes* (Stubblefield & Rothwell, 1981). Although neither *P. nathorstii* nor *Bothrodendrostrobus mundus* can be unequivocally assigned to the Chaloneriaceae without further information, these reproductive structures appear to have some isoetalean relationship (Leary & Mickle, 1989).

Some Late Carboniferous Gondwana lycopsids can also be compared to the isoetaleans. Cormose plant bases found in association with *Bumbudendron* Archangelsky et al. are similar to *Chaloneria*, *Cormophyton*, and Mesozoic *Pleuromeia*-like plants in known features (Archangelsky et al., 1981). Similar lycopsid occurrences have been noted by Pfefferkorn & Alleman (1989) in Carboniferous strata of Peru.

ANATOMICALLY PRESERVED TRIASSIC ISOETALAEANS

Recently, significant anatomical information was added to our knowledge of Mesozoic lycopsids, with the description of the Russian taxon *Takhtajanodoxa mirabilis* Snigirevskaya (Snigirevskaya, 1980a, b). This Triassic plant is an apparently unbranched lycopsid 13–15 cm long and 3–20 cm in diameter that produced a medullated protostele surrounded by a small amount of secondary xylem and had a lobed, sometimes bifurcating rhizomorphic base (Fig. 9I, Table 2; pl. I, 3 of Snigirevskaya, 1980a). *Takhtajanodoxa* is similar anatomically to Carboniferous lepidodendrids and the members of the Chaloneriaceae for which anatomy is known (*Chaloneria*; Pigg & Rothwell, 1983a; *Sporangiostrobus*; Leisman, 1970). For instance, it produced leaf bases with broad parichnos strands and wedges of fimbriate secondary xylem tracheids that alternate with aerenchymatous rays, a fertile region rather than a compact cone, and auriculate, trilete megaspores. Microspores are unknown. *Takhtajanodoxa* is distinguished from *Chaloneria* by elaborate ligules that extend basally into glosopodia (compare Fig. 10A, B; pl. V, 1 of Snigirevskaya, 1980a). In this respect *Takhtajanodoxa* is more similar to extant species of *Isoetes* than is any other anatomically preserved fossil form (Snigirevskaya, 1980a, b; Sharma & Singh, 1984). As in *Chaloneria*, transfusion tissue occurs in the region between the ligule and the vascular bundle in the leaf base. The anchor-shaped, sometimes branched rhizomorph of *Takhtajanodoxa* bears typical stigmarian rootlets and has irregular lateral

ridges resulting from secondary cortical tissue proliferation (Snigirevskaya, 1980a).

While Snigirevskaya (1980a, b) regarded *Takhtajanodoxa* as a member of a new order of lycopsids, the Takhtajanodoxales, Meyen (1987) suggested that this plant is probably related to the Isoetaceae. Thomas & Brack-Hanes (1984) placed the genus in the family Takhtajanodoxaceae in the Isoetales. *Takhtajanodoxa* differs from modern *Isoetes* in the production of an elongate stem, a radially symmetric rhizomorph, and the presence of sterile leaves. It cannot be compared in detail to *Pleuromeia*-type plants that lack anatomical features. Documentation of anatomically preserved ligules and parichnos strands in *Takhtajanodoxa* not only demonstrates heretofore uniquely *Isoetes*-like features in the Triassic, but also may prove valuable in interpreting the structure of leaf bases of other Angaran lycopsids previously thought to be eligulate (e.g., Meyen, 1972; Snigirevskaya, 1980a).

PLEUROMEIAN ISOETALAEANS—MESOZOIC AND CENOZOIC FORMS

In contrast to the recently recognized, anatomically preserved Carboniferous Chaloneriaceae, the larger isoetalean forms of the Mesozoic have been known for many years as compressions (e.g., *Pleuromeia*, *Cylostrobus* Helby & Martin, *Nathorstiana*, *Nathorstianella* (Figs. 4, 6, 9G, H, J, K; Table 2)). Traditionally, these plants represented the intermediate members of the lycopsid reduction series (Potonié, 1894; Mägdefrau, 1931; Hirmer, 1933). They are variously included in their own order, the Pleuromeiales (Delevoryas, 1962; Taylor, 1981; Gifford & Foster, 1989), their own family, the Pleuromeiaceae (Retallack, 1975; Thomas & Brack-Hanes, 1984; Meyen, 1987), in the Isoetales (Smith, 1938; Bierhorst, 1971), or the Lepidodendrales (Neuburg, 1960, 1961; Chaloner, 1967; Retallack, 1975; White, 1981). These plants remain share a number of similarities with the Carboniferous Chaloneriaceae (Tables 1, 2, 4). Unbranched or sparsely branched stems bear helically arranged vegetative leaves that typically have bilobed vascular strands and may possess parichnos (Neuburg, 1960, 1961; Kon'no, 1973; Dobruskina, 1974). *Pleuromeia*-type plants may bear rounded (e.g., *P. jiaochengensis*; Wang & Wang, 1982), anchor-shaped (*Cylomeia* White; White, 1981), or four-lobed (*P. sternbergi* Münster; Mägdefrau, 1931) rhizomorphic plant bases, all of which produce rooting appendages with stigmarian morphology (Kon'no, 1973; Retallack, 1975). Distally,

pleuromeians produce either a terminal cone (e.g., *Cylomeia*, *Skilliostrobos* Ash; Ash, 1979) or less compact fertile region (*Pleuromeia*), the latter sometimes described as pedunculate (Retallack, 1975). While fructifications of some species (e.g., *P. rossica* Neuburg, *Cylostrobos sydneyensis*) are clearly bisporangiate, those of other species (i.e., *P. sternbergi*, *P. obrutschewii* Elias, *P. jiao-chengensis*) are presumably monosporangiate. Isolated fructifications thought to belong in this group (Table 2) include *Cylostrobos* (Helby & Martin, 1965), *Austrostrobos* Morbelli & Petriella (Morbelli & Petriella, 1973) (which has been synonymized with *Cylostrobos* as *C. ornatus* (Morbelli & Petriella) Batten & Kovach; Batten & Kovach, 1990), *Skilliostrobos* (Ash, 1979), *Tomiostrabus* Neuburg (Sadovnikov, 1982a), and possibly the enigmatic *Cidarophyton* Chaloner & Turner (Chaloner & Turner, 1987).

In contrast to Carboniferous forms that have relatively simple sporangia, Triassic isoetaleans have sporangia that are sunken into the sporophylls (Fig. 10E). This morphology, coupled with compression preservation in which sporangial cavities are preserved as coalified casts, led to the initial interpretation that *Pleuromeia* sporangia were abaxial (Mägdefrau, 1931). Reinvestigations have demonstrated the adaxial, sunken position of sporangia of this taxon (Neuburg, 1960, 1961; Dobruskina, 1974; Retallack, 1975). Megaspores are assignable to such *sporae dispersae* taxa as *Banksisporites* Dettman, cf. *Triletes* (Erdtman) Potonié, and *Horstisporites* Potonié (Neuburg, 1960; Helby & Martin, 1965; Retallack, 1975; Ash, 1979). Like Carboniferous spores they are trilete, with a granulate to smooth (e.g., Krassilov & Zakharov, 1975) or reticulate (Ash, 1979) exine. Microspores of Southern Hemisphere taxa and some Russian and European forms including *Tomiostrabus* Neuburg and *Annalepis* Fliche have been assigned to the monolete taxon *Aratrisporites* Leschik *mut. char.* Playford & Dettman (Retallack, 1975; Ash, 1979). Although microspores of *P. rossica* were originally described as monolete, Neuburg (1961) demonstrated that these were degraded trilete grains that have a layered exine, the outermost layer of which is often missing (Neuburg, 1960, 1961). Spores of this type are referable to cf. *Punctatosporites* (Ibrahim) Potonié & Kremp. A transition from trilete to monolete microspores like those that characterize extant *Isoetes* thus occurred among some pleuromeians in the Triassic (Yaroshenko, 1985).

Pleuromeia-type plants known from compressions show a wide range of variation. The initially

described species, *P. sternbergi*, is known from Germany, France, Russia, and China (Fig. 9G, Table 2; Solms-Laubach, 1899; Seward, 1910; Mägdefrau, 1931; Hirmer, 1933; Neuburg, 1960; Chaloner, 1967; Fuchs et al., 1991). *Pleuromeia sternbergi* is characterized by a stem estimated to be about 1–2 m in maximum height and 5–10 cm in diameter and a plant base with four shortened rhizophoric lobes that bear stigmarian rootlet scars and attached rooting appendages (Mägdefrau, 1931). A terminal fructification 20 cm long is presumably monosporangiate and bears exclusively either micro- or megasporangia. This plant is reported to have produced basal leaves that were distinctly different from ones borne more distally (Fuchs et al., 1991).

The Russian species *P. rossica* is known in considerable detail (Fig. 9H, Table 2; Neuburg, 1960, 1961). In comparison to *P. sternbergi*, this Russian form is a smaller plant with a four-lobed rhizomorph with less extensive lobes. Parichnos strands are oval in comparison to the triangular strands of *P. sternbergi*, and fructifications are ovoid and bisporangiate rather than cylindrical and monosporangiate. Dobruskina (1985) recently proposed that *P. rossica* should be removed from the genus *Pleuromeia* and reassigned to a new genus, *Leiomeia*. The basis for this new genus is the apparent lack of sterile leaves in this taxon and the bisporangiate organization of the fructification (Dobruskina, 1985).

Other Russian forms include *P. obrutschewii*, *P. olenekensis* Krassilov, *P. taimyrica* Sadovnikov, and *P. jokvazhica* Dobruskina (Table 2; Krassilov & Zakharov, 1975; Sadovnikov, 1982b; Dobruskina, 1974, 1985). *Pleuromeia obrutschewii* is very similar to *P. sternbergi*, and according to Krassilov & Zakharov (1975) may be conspecific with the German taxon. *Pleuromeia olenekensis* can be distinguished from *P. sternbergi*, *P. rossica*, and other forms by its large (26 × 10 mm) megasporangia and large, reticulate megaspores (Krassilov & Zakharov, 1975). Megaspores have a three-layered wall, the outermost reticulate layer of which is easily removed from the spore body (Krassilov & Zakharov, 1975). Comparative study suggests that other taxa that lack the reticulate covering may bear similar spores that have become degraded during preservation. *Pleuromeia jokvazhica* is fairly well known from disarticulated vegetative and fertile remains, although details of plant base and spore types are obscure. Morphologically, this species is most similar to *P. sternbergi*, but has smaller and less compact fructifications (Dobruskina, 1985). *Pleuromeiopsis* Sixel

TABLE 2. Mesozoic isoetalean lycopsids. Data taken from the following sources: ¹ Snigirevskaya (1980a, b); ² Kon'no (1973); ^{3,4} Krassilov & Zakharov (1975); ⁵ Mägdefrau (1931), Fuchs et al. (1991); ⁶ Neuberg (1960, 1961); ⁷ Sadovnikov (1982b), Dobruskina (1985); ⁸ Dobruskina (1974, 1985); ⁹ Wang & Wang (1982); ¹⁰ Wang (1991); ¹¹ Retallack (1975); ¹² Helby & Martin (1965), Retallack (1975); ^{13,14} White (1981); ¹⁵ Ash (1979); ¹⁶ Morbelli & Petriella (1973), Retallack (1975); Batten & Kovach (1990); ¹⁷ Grauvogel-Stamm & Düringer (1983); ¹⁸ Bock (1962, 1969); ¹⁹ Bock (1962, 1969); ²⁰ Emmonds (1856), Brown (1958); ²¹ Walkom (1941); ²² Ash & Pigg (1991); ²³ Münster (1842).

Taxon	Age	Occurrence	Extent	Preservation	Stem length and width (cm)	Rhizomorph shape
<i>Takhtajanodoxa mirabilis</i> ¹	Early Triassic	Russia	Stem and plant base, megaspores	Petrification	13-15 × 3-20	Radially symmetric (forked)
<i>Pleuromeia hataii</i> ²	Early Triassic	Japan	Stem and plant base, megaspores	Compression	9.5 × 1.1-2.7	Forking, anchor-shaped
<i>Pleuromeia obrutschewii</i> ³	Early Triassic	Russia	Stem, fructification with megaspores	Compression	Unknown	Unknown
<i>Pleuromeia olenekensis</i> ⁴	Early Triassic	Russia	Fructification with megaspores	Compression	Unknown	Unknown
<i>Pleuromeia sternbergi</i> ⁵	Triassic	Germany, France, Russia, China	Stem and plant base, fructification with spores	Compression	100-200 × 5-10	Four-lobed
<i>Pleuromeia rossica</i> ⁶	Triassic	Russia	Stem and plant base, fructification with spores	Compression	100 × 4-5	Weakly developed four-lobed
<i>Pleuromeia taimyrica</i> ⁷	Triassic	Russia	Fructification	Compression	Unknown	Unknown
<i>Pleuromeia jokvazhica</i> ⁸	Triassic	Russia	Stem and plant base, fructification	Compression	>11 × 3-4	Unknown
<i>Pleuromeia jiaochengensis</i> ⁹	Triassic	China	Stem and plant base, fructification with megaspores	Compression	20-50 × 1.5	Tuberous
<i>Isoetes ermayinensis</i> ¹⁰	Middle Triassic	Northern China	Isolated sporophylls with attached sporangia containing spores	Compression	Unknown	Unknown
<i>Pleuromeia longicaulis</i> ¹¹	Triassic	Australia	Stem and plant base	Petrification	Unknown	Unlobed
<i>Cylostrobus sydneyensis</i> ¹²	Triassic	Australia	Fructification with spores	Compression	0.8-5.8	Unknown
<i>Cylomeia undulata</i> ¹³	Triassic	Australia	Stem, associated plant base	Compression	Unknown	?Anchor-shaped (associated)

TABLE 2. Continued.

Taxon	Age	Occurrence	Extent	Preservation	Stem length and width (cm)	Rhizomorph shape
<i>Cylomeia capillamentum</i> ¹⁴	Triassic	Australia	Stem with fructification, associated plant base	Compression	Unknown	?Anchor-shaped (associated)
<i>Skilliostrobus australis</i> ¹⁵	Triassic	Australia	Fructification with spores	Compression	1.5 × 2.5	Unknown
<i>Cylostrobus ornatus</i> ¹⁶	Triassic	Argentina	Fructification with megaspores	Petrifaction	Unknown	Unknown
<i>Annalepis zeilleri</i> ¹⁷	Triassic	France	Sporophylls with spores	Compression	Unknown	Unknown
<i>Lepacyclotes americana</i> ¹⁸	Late Triassic	Virginia, U.S.A.	Rosette of attached leaves	Compression	? × 0.8	Unknown
<i>Isoetes gramineoides</i> ¹⁹	Late Triassic	Pennsylvania, U.S.A.	Corm with attached roots, rosettes of leaves, isolated leaves and sporangia	Compression	0.8 × 1.2	Corm
<i>Isoetites circularis</i> ²⁰	Late Triassic	North Carolina and Arizona, U.S.A.	Corm with leaves, rosette of attached leaves	Compression	? × 10	Unknown
<i>Isoetites elegans</i> ²¹	Jurassic	Western Australia	Rosette of attached leaves, sporangia with megaspores	Compression	? × 4	Unknown
<i>Isoetites rolandii</i> ²²	Middle Jurassic	Idaho and Oregon, U.S.A.	Corm with attached leaves, sporophyll bases, sporangia, megaspores?	Compression	0.6 × 1.5	Rounded/lobed?
<i>Isoetites crocifformis</i> ²³	Late Jurassic	Germany	Corm (?)	Compression	Unknown	Lobed?

TABLE 2. Continued.

Taxon	Rhizomorph width (cm)	Fertile zone length × width (cm)	Size sporangium length × width (mm)	Microspores	Microspore size (μm)	Megaspores	Megaspore size (μm)
<i>Takhtajanodoxa mirabilis</i> ¹	3-20	Unknown	4-5	Unknown	Unknown	Unknown	300-500
<i>Pleuromeia hatai</i> ²	3	>14 × 4	19 × 8	Unknown	Unknown	cf. <i>Triletes</i>	650-700
<i>Pleuromeia obrutschewii</i> ³	Unknown	20 × 1.2-2.0	18-15	Unknown	Unknown	Unknown	370-390
<i>Pleuromeia olenekensis</i> ⁴	Unknown	Unknown	26 × 10	Unknown	Unknown	Unknown	990-1,120
<i>Pleuromeia sternbergi</i> ⁵	17	20 × 1.6-2.0	10-20	cf. <i>Laevigatosporites</i>	15-25	cf. <i>Triletes</i>	500-700
<i>Pleuromeia rossica</i> ⁶	Unknown	>3.5 × 3	Unknown	cf. <i>Punctatosporites</i>	Unknown	cf. <i>Triletes</i>	300-340
<i>Pleuromeia taimyrica</i> ⁷	Unknown	3.8 × 0.6-0.8	4-5 × 0.4-1.2	Unknown	Unknown	Unknown	Unknown
<i>Pleuromeia jokvazhica</i> ⁸	Unknown	3-8 × 6-12	2-20	Unknown	Unknown	Unknown	Unknown
<i>Pleuromeia jiaochengensis</i> ⁹	2.2	20 × ?	15 × 9	Unknown	Unknown	Unknown	300-500
<i>Isoetes ermayinensis</i> ¹⁰	Unknown	N/A	7-20 × 2-5	<i>Aratrisporites</i>	20-30	<i>Dijkstraisporites</i>	288-611
<i>Pleuromeia longicaulis</i> ¹¹	Unknown	Unknown	? × 7.5	Unknown	Unknown	Unknown	Unknown
<i>Cyclostrobus sydneyensis</i> ¹²	Unknown	0.8-5.8	Unknown	<i>Aratrisporites</i>	16-29	<i>Banksisporites</i>	350-512
<i>Cylomeia undulata</i> ¹³	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
<i>Cylomeia capillamentum</i> ¹⁴	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
<i>Skilliostrobus australis</i> ¹⁵	Unknown	1.5 × 2.5	10 × 2	<i>Aratrisporites</i>	27-38 × 36-40	<i>Horstisporites</i>	800-1,000
<i>Cylostrobus ornatus</i> ¹⁶	Unknown	? × 6	Unknown	Unknown	Unknown	Unknown	420-452
<i>Annalepis zeilleri</i> ¹⁷	Unknown	N/A	25-45 × 10-20	<i>Aratrisporites</i>	28-33	<i>Tenellisporites</i>	600-700
<i>Lepacyclotes americana</i> ¹⁸	3.8	N/A	Unknown	Unknown	Unknown	Unknown	400?
<i>Isoetes gramineoides</i> ¹⁹	Unknown	N/A	Unknown	Unknown	Unknown	Unknown	Unknown
<i>Isoetites circularis</i> ²⁰	Unknown	N/A	Unknown	Unknown	Unknown	Trilete	600-700
<i>Isoetites elegans</i> ²¹	Unknown	N/A	? × 1.2	Unknown	Unknown	Unknown	500
<i>Isoetites rolandii</i> ²²	2.5	N/A	10 × 10 associated	Unknown	Unknown	Round	440
<i>Isoetites crocifformis</i> ²³	Unknown	N/A	Unknown	Unknown	Unknown	Unknown	Unknown

was originally described to represent a somewhat larger *Pleuromeia* plant of about 3 m in height (Sixtel, 1962; see also Chaloner, 1967, and Dobruskina, 1974). Dobruskina (1974) reevaluated this material and concluded that the genus had been based on a mixed assemblage of several types of plants. She proposed the name *Ferganodendron* Dobruskina for the lycopsid stem segments that were a part of this assemblage (Dobruskina, 1974). The relationship of these forms to isoetaleans is not clear.

Evidence of pleuromeian plants is abundant in Australia. Bisporangiate fertile structures bearing *Aratrisporites* microspores and megaspores assignable to *Banksisporites* were described by Helby & Martin (1965) as three species of *Cylostrobus* on the basis of differential spore size. Retallack (1975) united these three species into *C. sydneyensis* and documented the co-occurrence of this fertile material with vegetative remains of *Pleuromeia longicaulis* (Table 2; Retallack, 1975). He further recognized the permineralized cone *Austrostrobus ornatus* (Morbelli & Petriella, 1973) from Patagonia as an additional species of *Cylostrobus*. White (1981) suggested that this taxon and several additional Australian species were distinctive from Northern Hemisphere forms and proposed the generic name *Cylomeia* for Australian pleuromeian plants (Figs. 4, 6, Table 2). Her primary criterion for this assignment is the more compact, conelike nature of the Southern Hemisphere forms, in contrast to the looser, elongate fructifications of the northern forms. White (1981) further suggested that the lycopsid cone genus *Skilliostrobus* (Table 2; Ash, 1979) might be the reproductive structure of some of the *Cylomeia* types. *Cidarophyton* is a globose lycopsid fossil that is difficult to identify unequivocally as cone, stem, or rhizomorph (Chaloner & Turner, 1987). However, this specimen bears strong resemblance to *Skilliostrobus*, and if it is a fructification, most probably also has pleuromeian affinities. Sadovnikov (1982a) has suggested that the genus *Skilliostrobus* be united with the Russian genus *Tomioostrobus*, on the basis of similar sporophyll and spore morphology.

Species of *Pleuromeia* are also known from Japan (Kon'no, 1973) and China (Wang & Wang, 1982). *Pleuromeia hataii* Kon'no from the Triassic of Japan is most similar to *P. sternbergi* based on the presence of monosporangiate cones and the morphology of the leaf bases, which also have triangular parichnos strands. The stem, however, is considerably smaller (3 cm in maximum diameter) and bears smaller stigmarian appendages that leave scars only 0.5–0.8 mm in diameter (Table 2;

Kon'no, 1973). The Chinese species *P. jiaochengensis* is characterized by entire, small plants 20–30 cm tall with swollen or tuberous rhizomorphs, and a large, terminal, spike-shaped strobilus (Fig. 9J, K, Table 2; Wang & Wang, 1982). Distinctive characters of *P. jiaochengensis* are the proportionally large fructification, sagittate sporophylls, and awl-like vegetative leaves. Isolated sporophylls assigned to *Annalepis* have been compared to species of *Pleuromeia* (Table 2; Grauvogel-Stamm & Düringer, 1983; Dobruskina, 1985; Meyen, 1987), and, more recently, to a newly described fossil species of *Isoetes* from the Cretaceous of northern China (Wang, 1991). Sporophylls of *Annalepis* bear large, elongate sporangia (2.5–4.5 × 1–2 cm) and have shortened distal laminae. Their fructifications are estimated to have been at least 14 cm wide (Grauvogel-Stamm & Düringer, 1983). Sporangia bear either trilete, spiny megaspores assignable to *Tenellisporites* Potonié or monolet *Aratrisporites* microspores. There is an intergradation in morphology between the sporophylls of *Pleuromeia*, *Annalepis*, and *Tomioostrobus*, and there is some suggestion these taxa might be congeneric (Dobruskina, 1985). Isolated sporophylls of *Lepacycloes* Emmons are also similar (Table 2; fig. 93 of Bock, 1969). Wang (1991) has stressed the similarities of *Annalepis* and *Tomioostrobus* to material from the Triassic of China that he has named *Isoetes ermayinensis* Wang. He suggested that these taxa are more similar to modern *Isoetes* than they are to Triassic pleuromeians. It is interesting, though, that these Triassic isolated sporophylls are also quite similar to Carboniferous genera such as *Lepidostrobopsis*, which they strikingly resemble (compare plate 3, fig. 1 of Grauvogel-Stamm & Düringer, 1983, with figs. 2, 3, of Abbott, 1963). This suggests that some morphological features are characteristic of the rhizomorphic lycopsids as a whole and cannot be used to unite subgroups within the clade.

Opinions vary on systematic positions of the pleuromeian plants and whether they should be recognized as one or several genera. The proposals by White (1981) for the establishment of the genus *Cylomeia* for Australian forms and by Dobruskina (1985) that *Leiomeia* be named for the Russian *Pleuromeia rossica* emphasize the variability among pleuromeians as a whole and, in both cases, reveal a strong biogeographic basis. The naming of these new genera may be justifiable but should rest on comparative study of material from all the widespread localities. Clearly, a reassessment of all taxa of pleuromeian forms is needed.

Younger, Cretaceous pleuromeian plants include

TABLE 3. Cretaceous and Tertiary isoetalean lycopsids. Data taken from the following sources: ¹ Mägdefrau (1932); ² Glaessner & Rao (1955); ³ Drinnan & Chambers (1986); ⁴ Krassilov (1982); ⁵ Saporta (1894), Teixeira (1948); ⁶ Bose & Roy (1963); Banerji (1988); ⁷ Bose & Roy (1963); ⁸ Brown (1939); ⁹ Brown (1939); ¹⁰ Skog & Hill (1992); ¹¹ Skog et al. (in press); ¹² Hill (1987).

Taxon	Age	Occurrence	Extent
<i>Nathorstiana arborea</i> ¹	Early Cretaceous	Germany	Stem and plant base
<i>Nathorstianella babbagensis</i> ²	Early Cretaceous	Australia	Stem and plant base
<i>Isoetes bulbiformis</i> ³	Early Cretaceous	Victoria, Australia	Corm with attached leaves
<i>Limnoniobe insignis</i> ⁴	Early Cretaceous (Aptian)	Mongolia	Stem and plant base, sporophylls, sporangia with megaspores
<i>Isoetites choffati</i> ⁵	Early Cretaceous	Portugal	Corm and attached roots, isolated sporophyll bases, sporangia, spores?
<i>Isoetites janaianus</i> ⁶	Early Cretaceous	India	Plant base with attached leaves and roots, microspores and megaspores
<i>Isoetites serratifolius</i> ⁷	Early Cretaceous	India	Isolated leaves
<i>Isoetites horridus</i> ⁸	Early Cretaceous– Paleocene	Western North America	Corm with attached leaves, megaspores
<i>Isoetites serratus</i> ⁹	Early Cretaceous– Paleocene	Wyoming, U.S.A.	Corm and roots, rosettes of leaves
<i>Isoetites</i> new species ¹⁰	Early Cretaceous	England	Plant base with attached leaves; megaspores
<i>Isoetites</i> new species ¹¹	Late Cretaceous (Cenomanian)	Kansas and Nebraska, U.S.A.	Corm with attached leaves
<i>Isoetes reticulata</i> ¹²	Late Oligo–Miocene	Tasmania, Australia	Isolated sporophylls, megaspores

the genera *Nathorstiana* (Table 3; Mägdefrau, 1932; Karrfalt, 1984) and *Nathorstianella* (Glaessner & Rao, 1955). *Nathorstiana* is known exclusively from a large collection of over 200 specimens of vegetative remains from Quedlinburg, Germany (Mägdefrau, 1932; Karrfalt, 1984). Included in this collection are both small, presumably young plants with radially symmetrical plant bases and larger forms with four-lobed bases that resemble those of extant species of *Isoetes* (Karrfalt, 1984). It has been suggested that this material documents ontogenetic variability within *Nathorstiana*, presumably showing that plants initially had radially symmetrical rooting meristems that underwent a developmental change to bilateral symmetry during their life history. This proposed ontogenetic change in symmetry in *Nathorstiana* is further cited as evidence for the homology of radially symmetrical forms such as *Stigmaria* and *Paurodendron* with bilaterally symmetrical, lobed forms such as *Isoetes* and *Protostigmaria* (Jennings et al., 1983; Karrfalt, 1984; Rothwell, 1984; Rothwell & Erwin, 1985).

Nathorstianella, a Late Cretaceous taxon, is known from Australia from a cast of a robust (18 × 4–7.1 cm) stem with four rounded lobes on its plant base (Table 3). It has been suggested (Glaessner & Rao, 1955) that *Nathorstianella* may be identical with remains described as *Isoetites elegans* Walkom (Walkom, 1941). As with the Devonian forms, the discovery of fertile remains would aid in clarification of early Cenozoic Isoetales.

Other lycopsids whose affinities remain obscure and which may or may not be related to isoetaleans include four types of remains: (1) compressed cones that resemble *Pleuromeia*, i.e., *Lycostrobus scotti* Nathorst (Nathorst, 1908); *L. longicaulis* Burges (Burges, 1935) and *L. chinleana* Daugherty (Daugherty, 1941); (2) permineralized lycopsid stems of unknown affinities, i.e., *Chinlea campii* Daugherty and *Osmundites walkeri* Daugherty; (3) the large-diametered stem impression *Isoetodendron striata* Bock (Bock, 1969); and (4) *Selaginella*-like forms with characteristic spore types, i.e., *Selaginellites hallei* Lundblad (Lundblad, 1950), and *S. polaris* Lundblad (Lundblad, 1948).

TABLE 3. Extended.

Preservation	Stem length and width (cm)	Rhizomorph shape	Rhizomorph width (cm)	Size sporangium length × width (mm)	Megaspore size (μm)
Compression	10 × 3.8	Four-lobed	1-4	Unknown	Unknown
Mold-cast	18 × 4-7.1	Four-lobed	5.5	Unknown	Unknown
Compression	4 × 3 (+ leaves)	Unknown	Unknown	Unknown	Unknown
Compression	5.0 × 3.0	Unknown	Unknown	Unknown	Unknown
Compression	? × 1	Bulbous	Unknown	7 (diameter)	700-1,000
Compression	14 × 5-7	Five-lobed	5-7	3.5-6 × 2-3 megasporangia 4-5.5 × 3.5-4 microsporangia	285-430
Compression	Unknown	Unknown	Unknown	10-12 × 3	Unknown
Compression	Unknown	Unknown	Unknown	Unknown	477-606
Compression	Unknown	Unknown	Unknown	Unknown	Present
Compression	Unknown	Bilobed	Unknown	Unknown	Unknown
Compression	6.4 × 4.0	Conical, unlobed	Unknown	Unknown	Unknown
Compression	Unknown	Unknown	Unknown	Unknown	606

Lycostrobus scotti is a bisporangiate cone from the Rhaetian of Sweden that is similar to *Polysporia* and *Sporangiostrobus* in having relatively large sporangia (1.5 cm long) with sporophylls that lack distal laminae (Nathorst, 1908; Chaloner, 1967). Megaspores are 550-600 μm and assignable to *Nathorstisporites hoplicus* Jung. Microspores are monolete, as are spores of the pleuromeians. They are compared with the genus *Chasmatosporites* Nilsson and *Aratrisporites*. This bisporangiate cone has little apparent organization to the distribution of mega- and microsporangia. Other species of *Lycostrobus* include *L. longicaulis*, with similar spores, from the Australian Triassic (Burgess, 1935) and *L. chinleyana* from the Triassic Chinle formation of Arizona (Daugherty, 1941). The assignment of these last remains to *Lycostrobus* is somewhat in doubt (Chaloner, 1967).

Chinlea campii Daugherty and *Osmundites walkeri* Daugherty also from the Chinle Formation, were originally recognized as an osmundaceous fern from the Petrified Forest of Arizona (Daugherty, 1941). These permineralized axes were reinter-

preted by Miller (1968) as lycopsids. He found them to be conspecific and united the two taxa under the name *C. campii*. Miller (1968) has further suggested that *Chinlea*, *Lycostrobus chinleyana*, and isolated *Lycopodites* leaves found together in the Chinle Formation could represent the same Triassic plant.

Isoetodendron striata Bock was named for an impression from the Upper Triassic of Virginia which Bock (1969) considered the remains of an arborescent lycopsid. It is not clear to me from the illustrated specimens what this material represents. The age and size of this fossil, together with the presence of trilete megaspores in the same matrix, suggest that *Isoetodendron* might represent a poorly preserved *Pleuromeia*-type plant found in a decortication state, but any taxonomic designations without further study seem premature.

Selaginellites hallei is of interest because although this plant has a megafossil habit similar to *Selaginella*, it bears spore types similar to those of the *Pleuromeia*-type plants (i.e., *Banksisporites pinguis* (Harris) Dettman and *Densosporites*

TABLE 4. Typical features of isoetalean lycopsids.

1. Heterospory, megaspore as propogule, often aquatic or semiaquatic reproductive biology.
2. Fructifications are bisporangiate (sometimes monosporangiate) fertile regions grading into cones—typically breaking up into dispersal units of sporophylls bearing sporangia.
3. Unbranched or sparsely branched stems—several centimeters to 2 m long.
4. Rounded or lobed rhizomorph.
5. Helically arranged microphyllous leaves with single or double vascular trace.
6. Parichnos/air channels in leaves.
7. Ligules present.
8. Leaf bases rather than leaf cushions, often nonabscising.
9. Rootlets with stigmarian anatomy borne in distinctive rhizotaxy.
10. Trilete megaspores.
11. Trilete or monolet microspores.
12. Endosporal megagametophytes.
13. Trabeculae/sterile tissue often present in eusporangium.
14. Secondary cortical proliferation, stems often preserved as decortication layers.

(Lundblad, 1950). Another species of *Selaginellites*, *S. polaris*, consists of a compressed cone and associated vegetative remains and also bears megaspores assignable to *B. pinguis* (Lundblad, 1950).

ISOETES-LIKE FORMS: MESOZOIC AND TERTIARY

Material described as *Isoetites* and *Isoetes* is the most similar in growth habit to the modern *Isoetes* (e.g., Figs. 1, 5, 7, 8, 9M; Bock, 1962, 1969; Brown, 1939, 1958, 1962; Drinnan & Chambers, 1986; Hill, 1987; Banerji, 1988; Ash & Pigg, 1991; Wang, 1991; Skog et al., in press; Skog & Hill, 1992). While most authors use the generic name *Isoetites* to designate fossil forms with an *Isoetes*-like habit, some (e.g., Bock, 1962, 1969; Drinnan & Chambers, 1986; Hill, 1987; Wang, 1991) prefer to equate fossils with the modern genus and name them as species of *Isoetes*. These fossils are widespread geographically and stratigraphically with approximately 16 species and over 30 occurrences represented from the Triassic to the Upper Tertiary (Tables 2, 3; Münster, 1842; Emmonds, 1856, 1857; Saporta, 1888, 1894; Fountaine, 1883, 1900; Seward, 1910; Brown, 1939, 1958, 1962; Daugherty, 1941; Teixeira, 1948; Bock, 1962, 1969; Bose & Roy, 1963; Krassilov, 1982; Drinnan & Chambers, 1986; Hill,

1987; Banerji, 1988; Ash & Pigg, 1991; Wang, 1991; Skog et al., in press; Skog & Hill, 1992). The considerable stratigraphic overlap between these smaller herbaceous forms recognized first in the Triassic, and the larger forms, which occur as late as the Lower Cretaceous (i.e., *Nathorstianella*; Glaessner & Rao, 1955) has always been problematic to the view of isoetalean evolution as a linear reduction sequence (Chaloner, 1967).

The genus *Isoetites* (Münster, 1842) was proposed for small cormlike plant bases that were referred to *I. crociformis* Münster (Table 3). This generic name was also used by Saporta (1894) for forms from France and Portugal he originally called *Isoetopsis* (Saporta, 1888) and also by Teixeira (1948) for the Portuguese fossils. Other *Isoetes* and *Isoetites*-like remains have been assigned to a variety of genera including *Yorkia* Wanner (Wanner, 1921; Bock, 1962, 1969), *Xantholithes propheticus* Ward (Ward, 1915), *Lepacycloes* (Daugherty, 1941), and *Limnoniobe insignis* Krassilov (Krassilov, 1982). Stems and their isolated sporophylls have been interpreted as grasses (*Yorkia*; Wanner, 1921; Bock, 1962), conifers (Emmonds, 1857), araucarians (Fountaine, 1883), cycads (Dawson, 1886), equisetoids (Fountaine, 1900), and bennettitaleans (Daugherty, 1941). Brown (1939, 1958, 1962) and Bock (1962) recognized the isoetalean affinities of these various fossils and renamed them as species of *Isoetites* or *Isoetes*, respectively (Ash & Pigg, 1991; Skog et al., in press). Vertically compressed specimens of *Isoetites* (Fig. 5) show radiating linear leaves surrounding an axis and are very similar in appearance to the vertically compressed specimens of the Australian pleuromeian plant *Cylomeia* (Fig. 4; White, 1981), or similarly preserved Carboniferous shoots (e.g., plate 28, figs. 1–4 of Abbott, 1963).

The most completely known *Isoetites*/*Isoetes* fossil plants are *Isoetites gramineoides* (Fig. 9L; Bock, 1962), *I. horridus* (Brown, 1939, 1962), *I. serratus* (Brown, 1939), *I. circularis* (Brown, 1958), *I. janaianus* (Banerji, 1988), *I. rolandii* (Ash & Pigg, 1991), *Isoetes bulbiformis* (Drinnan & Chambers, 1986), and *I. ermayinensis* (Wang, 1991). Because of their small size and probable in situ preservation, whole plants are often preserved (Bock, 1962; Brown, 1939; Drinnan & Chambers, 1986; Banerji, 1988; Ash & Pigg, 1991; Skog & Hill, 1992). Even when the morphology and anatomical details are not clear, a good idea of growth habit can often be obtained, especially from laterally compressed specimens (plate 14, fig. 1 of Bock, 1962; fig. 11B of Drinnan & Chambers,

1986; plate 1, fig. 11 of Banerji, 1988; fig. 2 of Ash & Pigg, 1991).

Information about the variability within this group has not been considered in detail. The most obvious variations within species of the fossil *Isoetes*/*Isoetites* group include details of plant size, and sporophyll and megaspore morphology. Leaf characters include the distinctiveness of vascular strand and air channels and presence and distribution of marginal teeth. Some species have completely or partly serrate margins (e.g., *I. serratus*, *I. serratifolium*, *I. circularis*), whereas leaves in others are entire-margined (e.g., *I. gramineoides*, *I. horridus*, *I. rolandii*). At least some of this vegetative variation may be explained by the differential preservational potential of different types of leaves. Some species of *Isoetes* and *Isoetites* have long, delicate, grasslike leaves, while others are quite strong and pointed (giving rise to the colloquial name "quillwort"). Presumably those more resistant leaves would be able to withstand the preservation process well enough to demonstrate the presence of rectangular pockets of air channels in their distal laminae (e.g., Fig. 7, *I. serratus*; *I. horridus*; Brown, 1939, 1962). On the other hand, in thinner and less resistant leaves, air channels and vascular strands are indistinct (Ash & Pigg, 1991). Megaspores are often found in situ or in direct association with isoetalean megafossils (Bock, 1962; Walkom, 1941; Bose & Roy, 1963; Hill, 1987; Banerji, 1988; Wang, 1991; Skog & Hill, 1992). Unfortunately, the in situ occurrence of microspores is especially rare (Banerji, 1988; Wang, 1991). In most cases they are poorly preserved, but in the best cases they can be identified to a *spora dispersae* species. For instance, spores similar to *Minerosporites dissimilis* were reported in situ in megafossils of *I. horridus* (Hickey, 1977). Other *spora dispersae* megaspore genera thought to have isoetalean affinities include several taxa from the Lower Cretaceous Dakota Formation of Kansas (Kovach & Dilcher, 1985, 1988). These include *Paxillitriletes vittanus* Kovach & Dilcher; *P. dakotaensis* (Hall) Hall & Nicolson, and *Minerosporites mirabilis* (Miner) Potonié and *M. dissimilis* Tschudy. These dispersed megaspores have been allied with the Isoetales on the basis of wall ultrastructure, spore morphology, and in some cases, correlation with similar spore types known in situ (Kovach & Dilcher, 1985, 1988).

With further investigation of Mesozoic and Cenozoic fossil *Isoetes*-type plants it may be possible to relate some fossil species to extant forms. Generally, extant *Isoetes* has posed difficulties for tax-

onomic study because of the lack of collections and the wide range of phenotypic plasticity (Hickey, 1986). Historically, leaf morphology, habitat preference, and megaspore ornamentation have been the primary characters used for classification (Pfeiffer, 1922; Hickey, 1986). Although recent studies show there is little cohesive correlation of systematically important characters, megaspore morphology does remain an important criterion (Hickey, 1986). Furthermore, because extant *Isoetes* species include many cases of hybridization and polyploidy (Hickey, 1986), interpretation of Mesozoic and Tertiary fossil species in a one-to-one relationship to extant forms is probably not tenable.

TRENDS WITHIN THE ISOETALEAN LINEAGE

A suite of morphological changes can be recognized in isoetalean lycopoids through time. These include a reduction in axial elongation, disappearance of vegetative leaf production (Fig. 1), trend from trilete to monoete microspores, production of a sunken adaxial sporangium with a velum (Fig. 10D), and elaboration of the basal portion of the ligule into a glossopodium (Fig. 10A, D, Table 5). It is interesting that, with the exception of the velum, all of these changes can be documented among forms that occur in the early Mesozoic. The earliest known plants with the small *Isoetes*-type growth habit occur in the Triassic of Pennsylvania (i.e., *Isoetes gramineoides*; Bock, 1969). Small plants lacking axial elongation (Fig. 9M) thus overlap in the Triassic with both larger "woody" plants of up to 2 m in height (*P. sternbergi*, Fig. 9G) and smaller forms with axially elongate stems (e.g., *P. jiaochengensis*, 20–30 cm tall, Fig. 9J, K). Monoete microspores are known in several species of *Pleuromeia* (Helby & Martin, 1965; Retallack, 1975), while other species retain trilete spores, and in still others spore morphology cannot be determined because degraded trilete spores may appear monoete (*P. rossica*; Neuburg, 1960, 1961). Sunken sporangia are common by the Mesozoic and occur in most of the *Pleuromeia*-type plants (Fig. 10E). Among fossil representatives, ligules with glossopodia are known exclusively in the permineralized Triassic *Takhtajanodoxa* (Fig. 10A; Snigirevskaya, 1980a, b). The presence of such structures has not been detected in compression taxa. Whether the absence of a velum among fossil isoetalean lycopoids is due to a lack of suitable preservation or because this structure evolved relatively recently cannot be determined at present.

It is interesting that the most obvious features

TABLE 5. Trends in the Mesozoic and Cenozoic Isoetales.

1. Reduction in axial elongation of the stem.
2. Reduction in amount of lateral growth.
3. Sporangia become increasingly sunken into sporophyll (*Pleuromeia* sporangia mistakenly thought to be abaxial).
4. Elaboration of ligular structure (glossopodium in *Takhtajanodoxa* and *Isoetes*).
5. Shift in microspore tetrad geometry resulting in change from trilete to monoete spores.
6. Decrease in number of vegetative leaves (most leaves of Isoetaceae are sporophylls).

in the stratigraphically youngest isoetaleans, the lack of axial elongation and vegetative leaves, have usually been considered as reductions, especially in reference to the traditional lycopsid reduction sequence (Fig. 1; Potonié, 1894; Mägdefrau, 1931; Stewart, 1947). In light of ontogenetic and evolutionary considerations, however, the process by which these "reductions" came into being may be more accurately considered a heterochronic process (Gould, 1977; Rothwell, 1987; DiMichele et al., 1989). Plants with the modern *Isoetes* growth habit effectively telescoped their life history by foregoing vegetative growth, stem elongation, and the production of vegetative leaves, and having an earlier onset of the reproductive phase of the life cycle. This life history was probably tied tightly to their frequently aquatic to marginal aquatic habitats and heterosporous reproduction (DiMichele et al., 1989). It would be interesting to consider further the environmental constraints that may have selected for this abbreviated vegetative sporophyte. One possibility might be the modification of the environment through competitive effects of other Mesozoic, and later, Cenozoic aquatic plants. Today, many species of *Isoetes* occur in disturbed habitats as pioneer species. Generally they compete poorly with aquatic angiosperms (W. Carl Taylor, pers. comm.). Isoetaleans may have been "driven" into restricted niche space by other plants.

Considered as a whole, isoetalean plants, whether Paleozoic, Mesozoic, or Cenozoic, have occupied a variety of ecologically similar types of environments. The Paleozoic Chaloneriaceae forms bearing characteristic spore types *Endosporites* and *Valvisporites* are known from both freshwater, clastic wetland, and peat-accumulating swamps (in deltaic lobes; Chaloner, 1958; DiMichele et al., 1979; Pigg & Rothwell, 1983a, b). The abundance of *Endosporites* and *Valvisporites* spores in the

basal zones of a coal and in thin bony coals (the "*Polysporia* marshlands" of Phillips & Peppers, 1984) may imply that at least in some cases, *Chaloneria* was acting as a pioneer species in the Pennsylvanian (Debra A. Willard, pers. comm.). In the Mesozoic, pleuromeian forms often grew in monotypic stands in environments interpreted as coastal margins (Retallack, 1975) and are frequently found in association with marine fossils (e.g., Kon'no, 1973; Retallack, 1975). Smaller, Triassic and Jurassic *Isoetes*-like fossils are also reported as monotypic deposits of matted leaves or isolated sporophylls (Ash & Pigg, 1991; Wang, 1991). Cenozoic isoetaleans occur in low diversity floras in aquatic, or fluvial, types of sedimentation. It may be that isoetaleans have acted as "pioneer species" in various habitats throughout their history (Debra A. Willard, pers. comm.).

ISOETALEAN LYCOPSIDS AND THE RHIZOMORPHIC CLADE

Isoetalean lycopsids can now be recognized as a long-ranging group that extends from the Paleozoic (Fig. 9, Tables 1–4). They were present possibly by the Devonian or Mississippian, but certainly well established by the Pennsylvanian, as demonstrated by the Chaloneriaceae (Pigg & Rothwell, 1983a, b). The group persisted into the Mesozoic, where some forms became reduced in size and complexity like modern *Isoetes*. Other forms with axially elongate stems persisted until at least the Lower Cretaceous. Some authors (e.g., Wang, 1991) have recently questioned the relationships of pleuromeians and *Isoetes* forms, since monopodial pleuromeians and plants with a modern *Isoetes* aspect are both well known in the Triassic. Although clearly an ancestor/descendant relationship does not exist between contemporaneously living Triassic plants, separate phylogenetic origins for plants displaying these two types of habit need not be invoked. In my opinion, the morphologically similar characters of pleuromeian and Triassic *Isoetes*/*Isoetites* forms outweigh differences in growth habit, and, until more distinct differences can be delimited, they remain part of a single, variable, plexus.

Recent research suggests that we can no longer look at the isoetaleans as a distinct lineage, but rather as a part of a more complex group of heterosporous lycopsids, perhaps a rhizomorphic clade (Rothwell & Erwin, 1985). This plexus shares many similarities of vegetative details including stelar and cortical anatomy, the production of stigmarian rootlets, secondarily derived bipolar growth, and

heterosporous reproductive structures. Further investigation in the following areas would greatly strengthen our understanding of the phylogeny of this group: (1) new information about reproductive structures and anatomy of late Devonian–Mississippian ancestral and/or early members of the isoetaleans; (2) understanding of the relationship of isoetalean and arborescent lepidodendrid radiations; (3) reexamination of the worldwide diversity of Mesozoic pleuromeian and *Isoetes* forms; (4) correlation of the ecology of extant *Isoetes* with the implied ecology and life history of fossil forms; and (5) formal phylogenetic analyses to test the strength of this proposed monophyletic group and its relationship to the rest of the Lycopoida.

The lycopsid reduction series has been a deeply entrenched concept in vascular plant evolution. However, with the removal of the constraints of thinking of rhizomorphic lycopsids as a linear transformation series, there is more room to consider this group as a plexus of related forms whose morphology reflects not only phylogeny, but also ecological constraints. Extant *Isoetes* clearly represents not a single homogeneous end product of a linear sequence, but the remnant of a morphologically variable mosaic that persisted in marginal aquatic environments since the Paleozoic.

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HABITAT, EVOLUTION, AND SPECIATION IN *ISOETES*^{1,2}

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ABSTRACT

Species of *Isoetes* are notorious for the difficulties they present in identification. These difficulties are attributable to a series of habitat adaptations that have resulted in morphological simplicity, homoplasy, and reticulate evolution. Internal air chambers in the leaves of all taxa indicate that primitive *Isoetes* was aquatic. During the breakup of Gondwana, ancestors of modern taxa appear to have passed through a terrestrialization phase, which was accompanied by development of several morphological novelties and reductions including the evolution of sclerotic phyllopodia. This adaptation appears to have evolved after separation of the Indian subcontinent. A new section of the subgenus *Isoetes* centered in India and possessing non-sclerified, persistent leaf bases is described. Following a terrestrialization phase, several lineages became secondarily aquatic and, in some instances, once again evolved a terrestrial habitat. As a result, the genus now occupies a variety of niches, from wholly aquatic to wholly terrestrial. Most terrestrial species, found as isolated populations of basic diploids, appear to be the result of gradual speciation via isolation and genetic divergence. Some aquatic species, often found in mixed populations containing taxa of different ploides, appear to have evolved abruptly via interspecific hybridization and chromosome doubling. Evidence from distribution patterns, megaspore morphology and viability, chromosome numbers, and electrophoretic profiles of leaf enzymes supports a hypothesis of allopolyploid speciation.

Isoetes L. is a cosmopolitan genus of heterosporous lycopsids comprising approximately 150 species. The generic limits of *Isoetes* are sharp, and while there is no difficulty in recognizing a plant as a member of the genus, there are difficulties with the identification of species and species relationships within it. Our studies indicate that these difficulties are attributable to (1) simplicity of form, (2) morphological convergence, and (3) allopolyploidy. Simplicity of form confounds species identification. Plants of *Isoetes*, often resembling tufts of grass, reveal few characters that can be used to distinguish species. Morphological convergence hinders phylogenetic reconstruction and obscures evolutionary relationships among species. Allopolyploidy results in a subtle mosaic of character state distributions, thus limiting our perception of both species and species relationships.

As a result of these difficulties, taxonomists of *Isoetes* traditionally have employed a simplistic approach to classification and phylogeny. Often single characters have been used as the primary basis for understanding the genus. Because students of *Isoetes* have had different points of view, their classification systems and species alliances have varied widely. For example, Pfeiffer (1922) revolutionized

Isoetes taxonomy by proposing a classification system based primarily on megaspore morphology. Her scheme replaced the earlier systems of Baker (1880) and Motelay & Vendryès (1882), which were based on habitat preference and concomitant morphological adaptations. Pfeiffer (1922) pointed out that many species are highly variable in their habitat preference. Furthermore, she argued that there is often little correlation between morphology (e.g., presence or absence of stomata and fibrous bundles in leaves) and habitat. Since many early collections of *Isoetes* lacked adequate habitat data, species were often assigned to these habitat sections based solely on their morphology, a situation that led to an artificial suite of relationships. Although Pfeiffer's system improved upon earlier classification schemes, it is still fraught with problems such as convergence, reduction, and polymorphisms (Hickey, 1986a).

The replacement of earlier classification systems based on habitat preference by Pfeiffer's classification based on spore morphology resulted in de-emphasizing habitat preference as a feature of taxonomic value. Today, not only is habitat preference again recognized as a valuable diagnostic character, but there is also considerable evidence indi-

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cating habitat preference has played a major role in the evolution of *Isoetes* at two levels: major phylogenetic change and recent speciation. In the first part of this paper we will show that habitat shifts have been responsible for a number of major morphogenetic changes. Many of these changes are quite ancient and the current geographic distribution of the various morphological states can best be understood using a vicariance model. In addition to these morphological changes, numerous reversions to the ancestral, aquatic habitat have resulted in homoplasy. The second part of this paper outlines the relationships between a species habitat preference and its gregariousness in nature, which in turn dictates the dominant mode of speciation, either divergence or allopolyploidy.

MAJOR PHYLOGENETIC CHANGE

The Isoetaceae (sensu Reed, 1953) can be characterized by the following synapomorphies: foliar embedded sporangia, labia, vela, indehiscent sporangia, trabeculae, multiflagellate sperm, lacunate leaves, and reduced axial growth. Based on these synapomorphies, the family represents a monophyletic assemblage that can be construed as primitively aquatic (Hickey, 1986b). Evidence supporting this contention comes from the presence of air chambers in the leaves of extant taxa and the fossil genus *Isoetites*. Such air chambers are generally regarded as providing buoyancy and an aeration mechanism for aquatic plants (Keeley, 1982). Certainly, the occurrence of air chambers in the leaves of all extant terrestrial *Isoetes* indicates that these plants had aquatic ancestors.

Isoetes includes species with alate leaves that are fully laminate and species with nonalate leaves that are nearly without blades. Alate leaves are universal in the Lepidodendrales, Lycopodiaceae, and Selaginellaceae, which are all close outgroups of the Isoetaceae. Therefore, alate leaves are inferred to be plesiomorphic in *Isoetes*. *Isoetites* may have arisen during the generally wetter conditions associated with the late Carboniferous and early Triassic. Species of *Isoetites* were alate. While the cosmopolitan distribution of this genus through the lower Tertiary suggests that it was rather successful, only three alate species have survived into modern times: *Isoetes baculata*, *I. gigantea*, and *I. bradei*. Of these, the latter two are probably now extinct. Together these three alate species of *Isoetes* and *Isoetites* represent *Isoetes* subgenus *Euphyllum* (Hickey, 1990). The other and far larger part of the genus, subgenus *Isoetes*, is characterized by a distal, three-dimensional subula and by alae that are restricted to the proximal portion

of the leaf. In addition, many species of subgenus *Isoetes* have leaves with supporting fibrous bundles in the leaf. Such bundles are not found in species of subg. *Euphyllum*. Both the subulate condition and the presence of peripheral fibrous bundles are potentially adaptive because they provide stability and mechanical support for leaves in habitats that are ephemerally aquatic or terrestrial (Hickey, 1986b). Radiation from aquatic habitats may have occurred in response to the generally warmer and drier environmental conditions since the Cretaceous. Nearly all extant species of *Isoetes* have retained this essentially terrestrial habit, although some have again reverted to an aquatic habitat.

The development of a terrestrial habit resulted in an early morphological and systematic radiation, which apparently occurred subsequent to the fragmentation of Pangea. The transition from homogeneous, stable, aquatic environments to seasonally dry, terrestrial habitats resulted in additional problems for *Isoetes*, in particular that of desiccation during arid periods. Species of *Isoetes* have adapted to this situation in two ways, both of which involve protecting the apical meristem during drought conditions. In one group of species, unmodified leaf bases are retained throughout the dry season and form a scarious protective layer about the apex of the corm. Such modifications in *Isoetes* appear to be uniquely derived and thus represent a synapomorphy for the associated species. In general, this clade is restricted to the Indian subcontinent (Hickey, 1986b).

The second manner of protecting the corm apex during drought involves the sclerification of leaf tissue. In some species, leaf primordia become sclerified and their growth is arrested. This results in scales similar to those found on branches of temperate deciduous angiosperms. *Isoetes nuttallii*, of western North America, produces such scales (Figs. 1, 2). In other species, portions of the leaf bases become sclerotic and remain after the non-sclerotic portions of the leaves have eroded. This produces a distinctive ring of sclerotic phyllopodia covering the apex. Such phyllopodia are most extensively developed in certain European and African species, but sclerotic phyllopodia are found also in the North American species *I. howellii* and *I. melanopoda* (Figs. 3, 4). The geographic and evolutionary relationships of the species involved strongly suggest that scales and phyllopodia represent two independently derived states for resistance to desiccation. Furthermore, the absence of species with sclerified scales and phyllopodia on the Indian subcontinent suggests that these synapomorphies originated in Gondwana after separation of the Indian subcontinent.